MECHANISM OF POLLINATION BY PHORIDAE (DIPTERA) IN SOME *HERRANIA* SPECIES (STERCULIACEAE) IN COSTA RICA

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Abstract.—The mechanism of pollination of *Herrania* flowers (Sterculiaceae) by phorid flies (Diptera: Phoridae) in Costa Rica is described in detail for the first time. Two undescribed phorid species, *Megaselia* sp. and *Dohrniphora* sp., are frequent visitors to the red or purple flowers of *H. purpurea* and *H. nitida,* and to the smaller, white flowers of *H. albiflora.* The flowers of all species are highly specialized for visitation and pollination by small-sized insects such as phorids. The behavior of the flies at the freshly-opened flowers indicates that they follow nectary cues and appear at flowers only at dawn and dusk when flowers exude a strong, musty (aminoid) scent and are most receptive for pollination. There appears to be some degree of coadaptation of flower morphology and phorid behavior suggesting phorids to be important pollinators of *Herrania.* Phorids land either upon the petaloid staminodes that form a barrier between the style and concealed anthers (in petal hoods or pouches) or on the long, dangling petal ligules of the hermaphroditic flowers. These insects enter the petal hoods, probably guided by stomate-type nectaries inside, and pick up large quantities of pollen on notal and head areas. Pollen-laden phorids often crawl through the central area of a flower, brushing the stigma and style and thereby causing pollination. Phorids may orient themselves towards the pistil area by elaboration of a scent from specialized trichomes or elaiophores on the ovary and basal area of the flower.

The purpose of this paper is to report for the first time the mechanism of effective pollination of *Herrania purpurea* (Pittier) R. E. Schultes, *H. albiflora* Goudot, and *H. nitida* (Poepp.) (Sterculiaceae, tribe Byttneriereae) by phorid flies (Diptera: Phoridae) in Costa Rica. Posnette (1944) observed phorids on *Herrania* flowers in Trinidad and suspected them to be pollinators. Cuatrecasas (1964) has summarized the floral, fruit, and vegetative characters that closely unite *Herrania* and *Theobroma* within the Byttneriereae. Although there has been considerable study of insect-mediated pollination in *T. cacao* L. ("cacao," "cocoa") for obvious economic reasons (e.g., Billes, 1941; Posnette, 1944; Soetardi, 1950; Glendinning, 1962; Hernandez, 1965, and many other papers), far less is known about the pollinators and pollination mechanisms of other *Theobroma* species and *Herrania* species. Given the great divergence in the size, coloration, and fragrance properties of flowers in both genera, it is most likely that very different groups of primary pollinators are involved. Various authors (e.g., Entwistle, 1972 and Bystrak and Wirth, 1978 give good reviews) have discussed the evidence favoring insect-

mediated pollination in *T. cacao,* in which the primary pollinators are believed to be certain genera and species of Ceratopogonidae (Diptera), based largely upon daytime studies in cacao plantations. In the present paper I describe the behavior of phorids that results in the pollination of *Herrania,* but do not rule out the possibility of other types of pollinating animals also being capable of such a process. Although phorid flies are known to be frequent visitors at many different flower species in the British Isles (Disney, 1980), little if anything has been determined as to their role as effective pollinators.

Methods and Materials

All of my observations on the three species of *Herrania* were carried out in a "garden" plot of these trees (Fig. 1) situated at "Finca Experimental La Lola," near Siquirres (10°06′N, 83°30′W), Limon Province, Costa Rica, a region of lowland tropical rain forest. The plot of *Herrania* (Fig. 1) was originally established about 25 years ago, amidst the cacao plantation of this locality. In two species, *H. purpurea* and *H. nitida,* both with showy blood-red to purplish flowers, inflorescences exude a distinctive musty scent which is even noticeable in withered, fallen flowers. The third species, *H. albiflora,* with smaller white flowers (Fig. 2), has no noticeable fragrance (when checked over a 24-hour period).

There is a total of 20 *H. purpurea* trees (D.B.H. range of 3.0–5.0 cm and height range of 1.8 to 4.5 meters) in the garden, 5 *H. albiflora* (D.B.H. range of 3.0–4.5 cm and height range of 2.4 to 4.0 meters) and 2 *H. nitida* (D.B.H. of 3.0 and 3.5 cm and heights of 3.2 and 4.0 meters), and all of these trees are arranged in rows. The area is either grazed by horses or cleared by periodic cutting (Fig. 1).

Observations on the abundance of new flower buds and open flowers on all of the *Herrania* trees in the garden area were made on the following dates: 21–22 July 1982, 8–10 December 1982, 25–27 February 1983 and 12–16 March 1983. February and March are relatively drier months at "La Lola" than are most other months, although daily light showers occur during these periods. From one to three days were spent during each of three periods (July and December 1982 and February–March 1983) making around-the-clock observations on the activity of insects at freshly-opened flowers of those species in bloom at the time. Nighttime observations, usually from 1900 to 2100 hours, were made with the use of red cellophane over a small flashlight. In addition to daytime observations, dawn-dusk observations consisted of observing flowers from about 0530 to 0800 hours and 1600 to 1830 hours. When insects were seen on the flowers, further observations were made on how they moved into the flower and exited from it. Care was taken to note the presence of pollen on the bodies of insects seen exiting from the flowers, and voucher collections were made for all insects found in the flowers. The observations allowed me to determine at what times of the day insects were most active at the flowers. Insects bearing pollen were examined carefully with a binocular dissecting microscope to determine if the pollen carried was that of *Herrania.* Samples of *Herrania* pollen were taken directly from flowers, although, since the pollen of related species of this genus are very similar (Taylor, 1965), I was unable to associate pollen on insects with each species of *Herrania* being studied.

Anthesis, pollen liberation, and periods of peak fragrance-release were examined by observing marked (with small color-capped pins) flowers of *H. purpurea* at
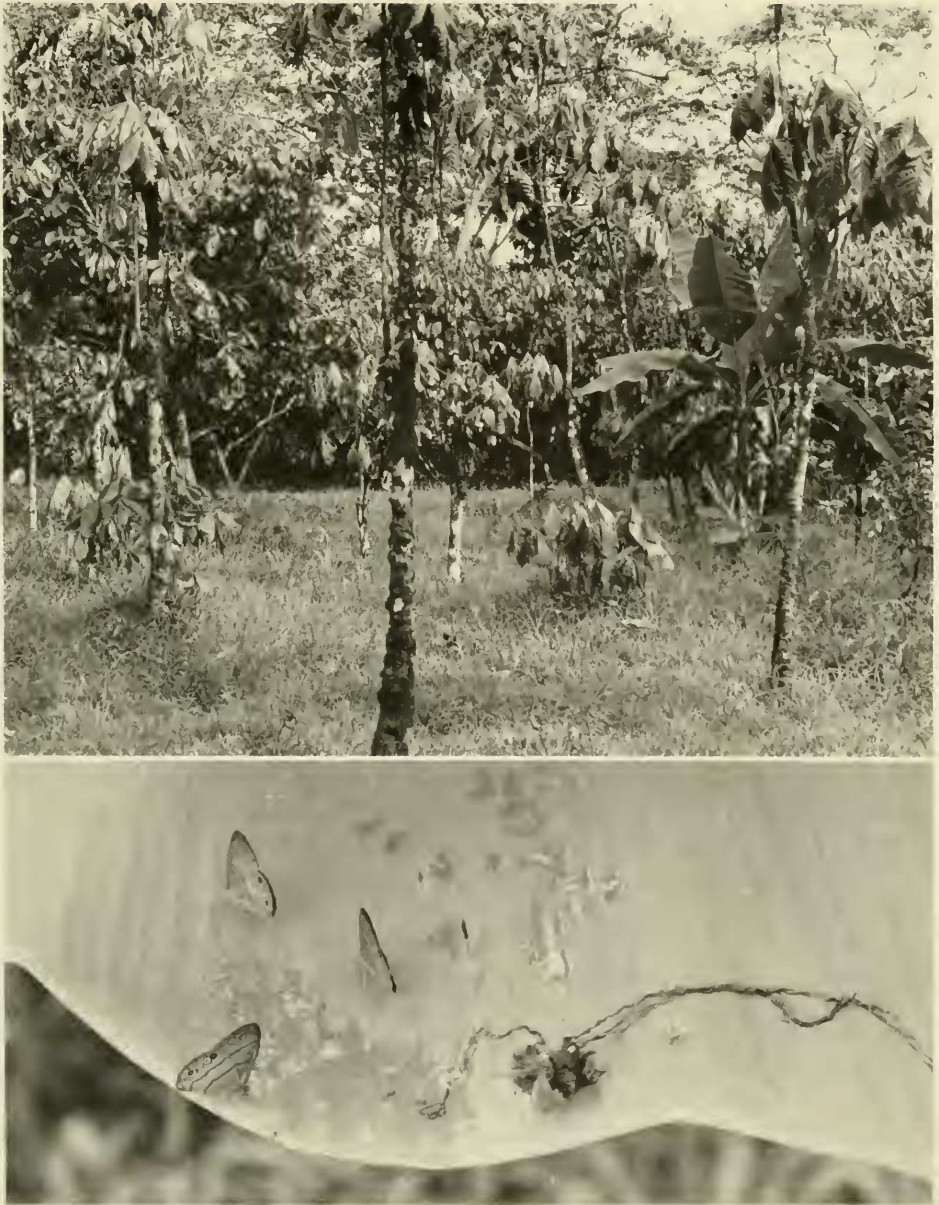
Fig. 1. The *Herrania* "garden" at Finca Experimental La Lola, near Siquirres, Limon Province, Costa Rica (top) showing the trees studied for phorid pollination, and satyrid butterflies feeding on fluids exuded from rotting *H. purpurea* flower fallen on a *Heliconia* leaf (below). Note the very elongate petal ligules of the dead flower.

various times of the day and night. The flowers were also checked at various times over a 24-hour period to determine if liberal amounts of nectar could be seen in them, and if so, the locations. Finally, I collected several specimens of *H. purpurea* for preliminary scanning electron microscopy: an examination was made of floral parts, including: pistil and ovary, petaloid staminodes, ligules associated with

petals, stamens and anthers. Emphasis was placed on detecting possible nectaries and glandular hairs (trichomes) responsible for fragrances. The electron micros-copy was carried out at the Great Lakes Center associated with the University of Wisconsin–Milwaukee, and details of the methods used are summarized elsewhere (Young et al., 1984). An examination of pollen and location of pollen grains was also made.

General observations on the condition of flowers at various times of the day were also made, with an emphasis on comparing activity of pollinators at flowers in drier and wetter periods.

<div align="center">RESULTS</div>

Phenological notes.—During July 1982, intense flowering was noted in *H. pur-purea,* and to a lesser extent in *H. albiflora.* Fifteen of 20 *H. purpurea* had full-sized floral buds and open flowers at that time. A pronounced difference in the abundance of flowers on trees of both species was found between late rainy season (December 1982) and mid-dry season (February 1983) censuses, with a sizable reduction in flowering in the latter period (Table 1). Although these samples were limited to rather short census periods, I believe that they represent real biological differences in flowering patterns, judging also from the presence or absence of smaller flower buds and fruits (to be summarized in a later paper). For the purposes of the present paper, I assume that the observed differences are representative of temporal changes in flowering intensity in both species, and particularly for *H. purpurea,* which provided the largest sample. Additionally, one of the two *H. nitida* trees had 106 buds (in various stages of development as judged by size differences) and two freshly-opened flowers on 13 March 1983. As noted in Table 1, there is considerable variation in the numbers of flowers on individual trees, but during both census periods, flower buds were more numerous than open flowers. Development of new buds may be rapid, since one *H. nitida* tree on 26 February 1983 had 40 buds and no open flowers, and about two weeks later (13 March) the number of buds had more than doubled. Daily output of freshly-opened flowers on *Herrania* trees is very low, ranging from one to five in most cases. During the dry period, successful rainy days precede "bursts" of flowering in *H. purpurea.* For example, following three days in which there was moderate rainfall for two to six hours each day, three of the 20 trees had a combined total of 40 new buds and four freshly-opened flowers. Prior to this, all of these trees had practically no large buds and open flowers.

A phenological pattern for adult *Herrania* trees at this locality can be tentatively derived from the most extensive data set available, that of *H. purpurea.* During the rainy season there is a very high abundance of new flower buds and with a daily output of a few open flowers in each inflorescence on each tree. Flowering, as suggested by casual observations in July 1982, most likely "peaks" during the middle of the rainy season, but there is some flowering throughout the year on many individual trees. A greater percentage of trees are in flower during the rainy season than in the drier period. During the drier period ("veranillo") flowering is greatly reduced, but small bursts occur when there are several successive days of moderate rainfall. I view month-to-month flowering in these trees to be a very fluid phenomenon, governed largely by influence of rainfall and other environ-mental factors on internal physiological systems related to fruit development and

Table 1. Abundance of flower buds and open flowers on two species of *Herrania* (Sterculiaceae) at different times of the year at "Finca Experimental La Lola," near Siquirres, Limon Province, Costa Rica.

Census Period	Season	Numbers of Flowers on *Herrania* Trees							
		H. purpurea (n = 20 trees)				*H. albiflora* (n = 5 trees)			
		Total Open Flowers	$\bar{x} \pm SD$	Total Buds	$\bar{x} \pm SD$	Total Open Flowers	$\bar{x} \pm SD$	Total Buds	$\bar{x} \pm SD$
10 Dec. 1982	Late rainy	17	1.41 ± 3.44	213	21.25 ± 22.27	8	0.84 ± 1.32	87	11.61 ± 9
26 Feb. 1983	Dry	1	—	38	1.95 ± 3.74	0	—	9	1.50 ± 2

The range in numbers of flower buds and open flowers on *H. purpurea* trees was 0–64 and 0–12 respectively during the late rainy season census, and 1–5 for buds during the subsequent dry season census. During the late rainy season the height range for flowers was 0.24 to 4.80 meters while during the dry season it was 0.1 to 2.1 meters on these 3–4 meter tall trees. For *H. albiflora* during the late rainy season there was a range of 12–20 buds per tree and during both seasons flowers were 0.1 to 2.0 meters on trunks 2 to 3 meters high.

Following a few rainy days in March 1983, 3 trees of *H. purpurea* had a combined total of 40 buds and 4 open flowers, one *H. albiflora* had 3 buds and 2 open flowers, and one of 2 *H. nitida* had 107 buds and 2 open flowers.

maturation. During the dry season, for example, *H. purpurea* trees are loaded with very high numbers of mature fruit (A. M. Young, unpublished observations), a time of relatively low flowering. Less extensive data from other *Herrania* at this locality suggest similar phenological patterns.

Diurnal flowering pattern.—In all three species, full-sized flower buds begin to split open usually after dark but before 2000 hours, and flowers are fully open by 0600 to 0800 hours the following day. During the rainy season, buds sometimes begin splitting open between 1600 and 1800 hours. These conclusions are drawn from (1) following the opening patterns of a total of 32 *H. purpurea* flowers (27 in December 1982 and 5 in March 1983) and four *H. nitida* flowers (March 1983), and (2) casual observations at various times of the day and night on flowers of all three species. If flowers are not pollinated on the day of opening, they often wither and fall off by the following evening, and during the dry season flower drop even occurs in the afternoon hours in hot, dry weather. Freshly-opened flowers have maximal fragrance from about 0600 to 0900 hours, and during the rainy season, if they are still on trees, a second period of fragrance from about 1600 to 1900 hours.

Anthers fully dehisce during the morning and afternoon hours in the rainy season. But during the dry season, anthers of all three species fully dehisce much earlier in the morning, very soon after flowers are fully open. Freshly open flowers have no signs of copious nectar flow at any time of the day, nor is there a noticeable crepuscular cycle of generous nectar production. During the daytime, the inner surfaces of petal hoods of *H. purpurea,* particularly in the rainy season, are often coated with patches of liberated pollen, easily spotted by the creamy white to yellow color of pollen against the dark red or purplish tissue.

Evidence of phorid pollination.—During the rainy season in particular, fallen withered flowers of *H. purpurea* attract a variety of juice-feeding insects, including

satyrid butterflies (Fig. 1), presumably lured by the strong musty scent which is associated with both fresh and withered flowers. Occasionally cecidomyiid midges are seen resting on exposed floral parts of *H. purpurea* during the rainy season, but their numbers are very low and visitations number only four out of approximately 65 insect-flower observations. In spite of lengthy observations when these insects were found on flowers, these midges were never seen to enter into the central style area or peripheral petal hoods. Leaf cutter ants, *Atta* spp., are frequent severe defoliators of the leaves and flowers of *Herrania* at this locality. At least three species of ants occasionally visit the flowers. Other dipterans observed occasionally at open flowers include *Bradysia* (Sciaridae). None of these organisms, however, exhibit the regular behavior of visiting open flowers in high frequency and in the numbers observed for phorids. No bees were seen on flowers of any *Herrania* species at this locality, and observations were made at various times of the day and night, including the 0400 to 0700 hours when certain groups of pre-dawn bees (e.g., *Ptiloglossa*-Colletidae and some Halictidae) are active.

By far the most abundant insect on the flowers of all three species during both rainy and dry seasons were flies (body length 4–7 mm) of the family Phoridae. Two undescribed species from genera, *Megaselia* and *Dohrniphora*, were recorded from *Herrania* flowers. Unfortunately it was not possible to determine species for the phorid genera collected from *Herrania*, largely because all specimens were female and it is virtually impossible to make species determinations with females (e.g., Disney, 1981).

During the rainy season (July and December 1982 periods), from one to six phorids were observed simultaneously on a single flower of *H. purpurea*. Individuals of both genera were only observed at the flowers during the early morning period (0600 to 0730 hours) and late afternoon to dusk (1650 to 1800 hours), suggesting a strongly crepuscular activity pattern associated with flowering activity *H. purpurea*. During the dry season observations (March 1983) several phorids were found on the few *H. nitida* flowers and *H. albiflora* flowers, but only during the early morning hours (0600 to 0730 hours). Whereas during the rainy season the flies were regular visitors to freshly-opened and roughly 8-hour-old flowers on a daily basis, during the dry season there was considerable day-to-day variation in their occurrence, and on mornings, they are totally absent. Although another phorid genus, *Chonocephalus*, was found breeding in rotting cacao pods very close to the garden near the end of the dry season in 1982 (late March and early April), none of these were found on *Herrania* flowers. Judging from voucher samples collected from flowers, the abundance of *Megaselia* and *Dohrniphora* species was very similar. Each genus was represented by one undescribed species.

Pollinating activity of these phorids was indicated by the repeated observation of individual flies entering petal hoods without pollen on their bodies, and then exiting, usually from 4 to 15 seconds later, with generous amounts of pollen on the notum and head. The pollen was visible against the dark background color of these bristle-covered flies. Upon exiting from a flower in this manner, a phorid would fly to another flower on the same inflorescence, or, more frequently, leave the observation site. Several observations were made of phorids, laden with pollen, moving through the central area of the flower, brushing against the style and then either (a) flying away, or (b) squeezing between the petaloid staminodes and re-entering a petal hood. Two approach patterns to open flowers were repeatedly

Fig. 2. Top, left to right: inflorescence of *H. purpurea* showing open flowers and large (full-size) floral buds (left) and view of a freshly-opened flower showing the petaloid staminodes and proximal sections of petal ligules. Below, left to right: *H. purpurea* with petal hoods held open to expose the light-colored anthers and pollen; freshly-opened flowers of *H. albiflora*.

observed: (a) most frequently, phorids would alight on the elongate, suspended ligules and rapidly crawl up to the flower and enter it; (b) phorids would land directly on a petaloid staminode and enter the flower. All movements were rapid, characterized by a typical "jerky" walking pattern common to phorids. On several
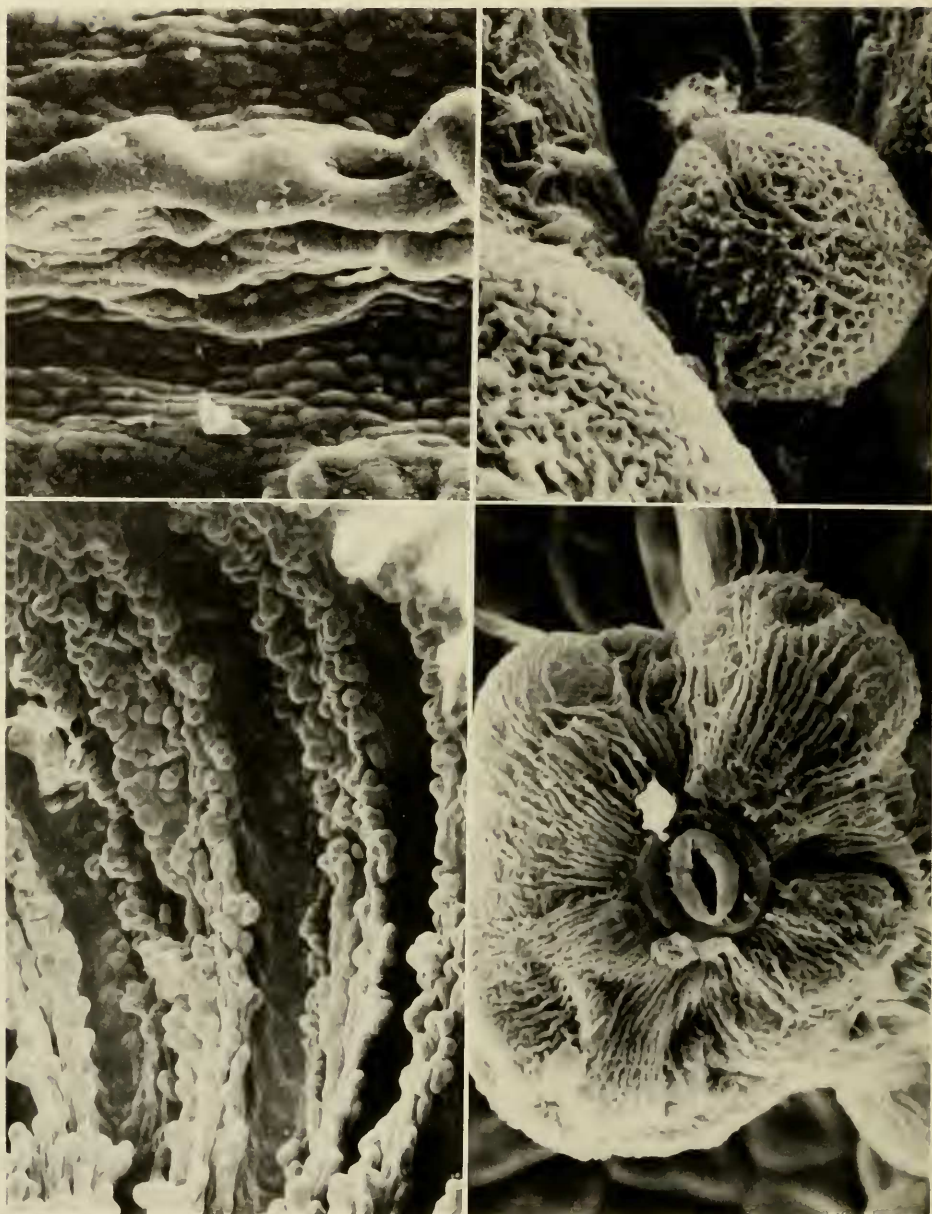
Fig. 3.   Scanning electron microscope photographs of the petal ligule and petal hood floral parts in *H. purpurea*. Top, left to right: ridge of intertwining bulbous cells forming a pronounced ridge on concave (adaxial) surface (left) (180×), and *H. purpurea* pollen grain (1800×) lodged between sulci of convex (abaxial) surface. Below, left to right: inner surface of petal hood (27×) in vicinity of anther sacs, and showing distinct ridges of bulbous cells, possibly nectar guides; a stomate-type nectary (630×) opening between bulbous cells of previous photograph.

occasions, phorids would land on ligules and then fly away, without entering the flower. Phorids did not alight on closed buds in inflorescences or on adjacent bark or moss. Frequently, several phorids would show up at a flower at about the same time, and depart in the same manner. A total of eight phorids were collected from
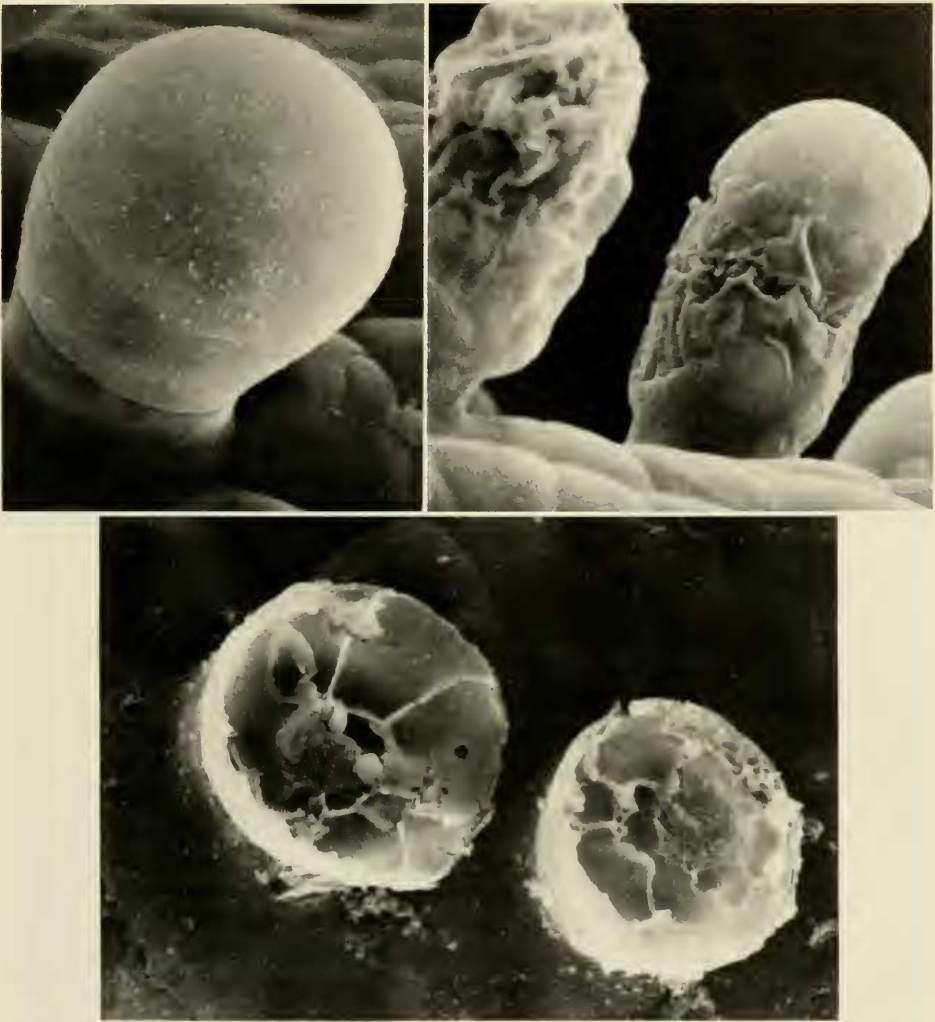
Fig. 4. Suspected elaiophores or oil (fragrance)-secreting trichomes on the surface of the ovary in *H. purpurea*. Top, left to right: short, bulbous elaiophore or trichome (2520×), possibly a young developmental stage, and elongate elaiophore or secretory structure (1800×) with convoluted surface. Lower: basal area of possibly chewed- or broken-off elaiophore or secretory trichome (252×).

Herrania flowers, although many more were observed, and of these, all were female and six had pollen on their bodies. Pollen deposition on the stigma and style of *H. purpurea* is of the scattered or "smear" type (Fig. 3), and involves the placement of many pollen grains (range of 15–95) by a single phorid on one visit to the style area. Germination of pollen on the style, in addition to the stigma, is common in all three species of *Herrania* studied (Fig. 3). Fully-dehisced anther sacs (Fig. 3) characterize virtually all open flowers by 1500 hours on the day they open.

    The highly convoluted surfaces of the ligules of *H. purpurea* (Fig. 4) are probably glandular. Pollen grains (Fig. 4) are lodged on the ligule surface, presumably by phorids exiting petal hoods after brushing against dehisced anthers, and grains

are also scattered on the inner surface of the petal hoods (Fig. 4), the site of stomate-type nectaries (Fig. 4). The range in number of pollen grains found adhering to the inner surface of petal hoods following a peak period of anther dehiscence is 58 to 430 for a total of n = 25 petal hoods examined. The exine of *H. purpurea* pollen grains is moderately sculptured (Fig. 4), a condition related to the ability of grains to lodge both on the sides of petal hoods and in the bristles of phorids and other insects. The surface of the ovary and basal area of the flower of *H. purpurea* has many peg-like rounded projections, presumably glandular trichomes or elaiophores producing fragrance compounds or nutritive substances attractive to insects (Fig. 5). These structures include both small, almost bulblike projections with smooth surface as well as elongate ones with convoluted surface (Fig. 5). It is frequently found that the ovary surface has "bare" patches where some of these structures appear to have been broken off or chewed off (Fig. 5). When phorids come into contact with the style, they sometimes orient headdownwards towards these structures on the ovary surface. Movements of phorids in the flowers are so rapid that I was unable to determine if they had contact with these structures.

DISCUSSION

The results reported in this paper suggest the following pollination mechanism in *Herrania* species at "La Lola" in Costa Rica. Flowers open primarily just before dawn and anthers dehisce shortly thereafter. At the time of opening flowers exude a strong musty (aminoid) scent that attracts large numbers of phorid flies (*Megaselia* and *Dohrniphora* species), all females. As noted by Percival (1965) for other fly-pollinated plants, the phorids are attracted to the dangling, elongate petal ligules, which initially function as a landing site for pollinators. Pollination then takes place in the manner described above. Pollination in both *Theobroma* and *Herrania* can result from pollen grains being deposited in this manner (Cuatrecasas, 1964). Orientation of phorids to the style area may be enhanced by the liberation of suspected fragrance compounds or nutrients associated with the glandular trichomes or elaiophores (see Simpson and Neff, 1981) coating the ovary and basal area of the flower. During the mid-morning and afternoon hours, phorids are absent from the flowers. During the rainy season, flowers often remain fresh in appearance by dusk of the same day of opening, and fragrance is again detected at this time of the day. There is a second pulse of phorid activity at these flowers, and additional pollination may occur. Dusk visitation may allow phorids to pick up payloads of pollen which are then used to pollinate freshly-opened flowers the following day. If this is the case, *Herrania* flowers may exhibit, particularly during the rainy season, overlapping pistillate and staminate phases (e.g., Baskin et al., 1981; Bawa and Beach, 1981), although confirmation of such patterns awaits further study.

The closely related Bombacaceae often have tufts of nectaries at the base of the sepals and are bat-pollinated (Cronquist, 1981). Pollination systems involving flies may also involve the positioning of a floral reward system at the base of the flower (e.g., Philbrick, 1983). Simpson and Neff (1981) describe the nutritive oils secreted by specialized glandular tissue in the Solanaceae, which provide a lipid-rich reward for bees to feed to their young. Stomate-type nectaries, of the kind found on the inner surface of the petal hoods, are known from a variety of plants
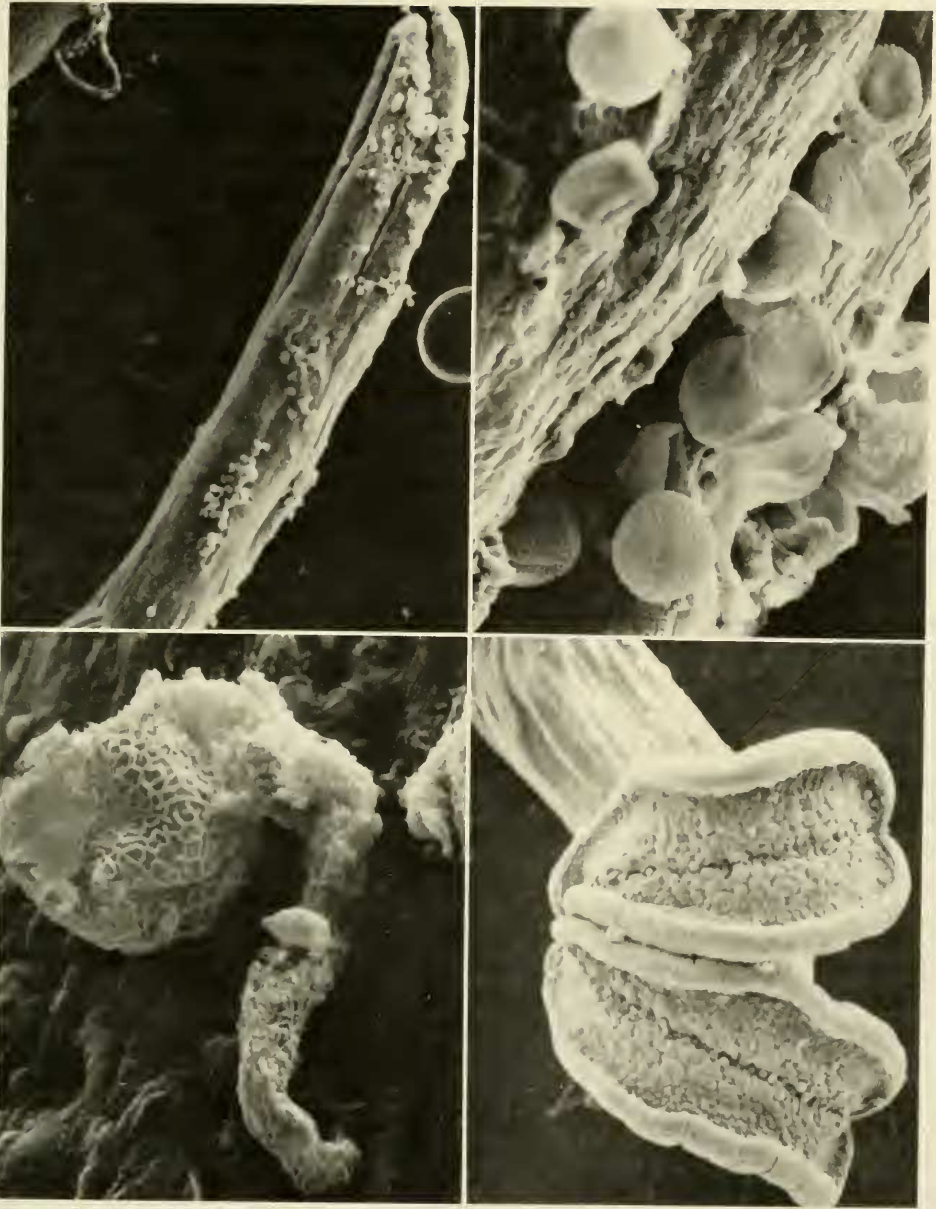
Fig. 5.   Pollen distribution and pollen tube growth on the style of *H. purpurea* and dehisced anthers. Top, left to right: natural distribution of pollen grains, presumably a "smear" from one or more phorids (Diptera) along the style (left, 50×) and closeup of lodged pollen grains (right, 630×). Note sculptured exine of pollen grains, also seen in Fig. 3. Below: germination of a pollen grain on the style (1440×) and dehisced anthers with all but a few pollen grains liberated (45×).

(e.g., Fahn, 1979). Kevan and Baker (1983) mention that the short proboscis of dipterans is adapted to getting nectar from shallow areas on floral parts. Phorids may extend their probosci into the stomate-type nectaries for feeding. In a related study (Young et al., 1984), stomate-type nectaries were found in *Theobroma* species

as well, not only on the petal hoods but also on the petal ligules. Further studies will focus upon the determination of the secretory functions of these structures in both genera. Tentatively I assume that the available data indicate a pollinator-reward system located primarily in two areas of *Herrania* flowers: (a) nectaries scattered on the inside of the petal hood, and (b) secretory structures located on the ovary and also in the basal area. The behavior of phorid flies in *Herrania* flowers is such that they come into contact with these areas of the flower, and in doing so, (a) pick up pollen and (b) smear pollen on the stigma and style. To what extent any of the *Herrania* species are self-compatible awaits an experimental approach. But some indirect data suggest that self-compatibility might exist: (a) there is very high fruit set on individual trees, as noted primarily for *H. purpurea,* (b) most trees bear fruit, and (c) in instances in which only one individual has flowers (such as seen in *H. albiflora*) this tree subsequently has fruit. Such observations cannot rule out the possibility of pollen being obtained from trees outside the garden area (which is highly unlikely, since all of the trees at "La Lola" are planted, i.e., introduced), and that there is some inter-tree transfer of pollen within the garden plot. Although both in wild and cultivated *Theobroma* cacao fruit set on a per tree basis is often low, lowest yields are typical of self-incompatible varieties.

The markedly crepuscular activity of phorids at *Herrania* flowers is most likely related to (a) the synchronization of anthesis with pollinator activity, and (b) ecological constraints for small-bodied, dark-colored flies to be active during the hottest hours of the day. Dusk pollination systems in the tropics involving small insects may be more frequent than previously believed (e.g., Gibbs et al., 1977), and it is physiologically less stressful for small dark-colored flies to be active early and late in the day (Willmer, 1982). To what extent discovery of receptive *Herrania* flowers at dawn and dusk is related to how phorids perceive color remains unknown, although certainly the strong scent of *H. purpurea* and *H. nitida* play major roles. Percival (1965) reports that flowers with full-red or purple colors and aminoid scents are usually fly-pollinated, although such adaptations, in conjunction with other floral features, are also found in bat-pollinated plants in the tropics (e.g., Steiner, 1983). The moderately-sculptured exine of *Herrania* pollen is consistent with insect-mediated pollination, particularly when contrasted to the very smooth-surfaced pollen grains of a wind-pollinated rain forest understory tree in Costa Rica (see Bawa and Crisp, 1980). *Herrania* pollen falls into the type adapted for insect vectors (Heslop-Harrison, 1979). The presence of what appear to be nectaries and other glandular structures, and a strong scent in at least two of the species studied, all point to a pollination system involving animals.

Posnette (1944) called attention to the probable role of phorids in *Herrania* pollination, and noted that at least some *Theobroma* species had very different dipteran pollinators (namely Ceratopogonidae). Phorids such as *Megaselia* are known to breed in various kinds of plant and animal debris (e.g., Disney and Evans, 1982; Villa, 1980; A. M. Young, unpublished field data) as well as in fungi and other microhabitats (Disney, 1982a, b). Similar to what Villa (1980) found for *M. scalaris* (Loew) feeding in the larval stage upon rotting amphibian eggs in Nicaragua, I have found larvae of this species in rotting larvae of the social paper wasp *Polybia simillima* Smith in Costa Rican rain forest. Phorids such as *M. scalaris* and other *Megaselia* species that undergo their life cycles in carrion (e.g.,

Kneidel, 1983) might be attracted to flowers with strong aminoid or carrion-like fragrances (e.g., *Herrania*). In general, phorids associated with *Herrania* flowers most likely breed in the damp, shaded understory of rain forest and some kinds of agricultural habitats such as well-shaded cacao. *Herrania* very likely evolved along streams in lowland Neotropical rain forests (e.g., Cuatrecasas, 1964; J. Leon, unpublished manuscript) in partially-shaded habitats, and such habitats may also have been suitable for pollinators such as the Phoridae. When *Herrania* is grown in an open garden plot situation as seen at "La Lola," influences of the dry season may be greater than would be expected in the natural habitat, and one manifestation is the rapid wilting of flowers prior to dusk on the day they open.

My preliminary data suggest that *Herrania* species are pollinated principally by phorids. The observed phenological patterns of flowering would suggest that the interaction is highly unspecialized, since phorids would not have sufficient floral resources available throughout the year. In natural habitats however, the association might be more stable throughout the year, particularly in rain forests where understory trees might not experience the effects of dry periods as much as canopy species. As a basis for further experimental studies, the following discussion is therefore offered.

Some dipterans have specialized pollination associations with plants (e.g., Warmke, 1952; Percival, 1965; Kevan and Baker, 1983). The floral structure of *Herrania,* in which both pollen and presumed floral rewards are highly concealed within the flower, warrants a specialized pollinator, and the behavior of phorids in the flowers suggests such an association. Yet to what extent phorids are specialized to be *Herrania* pollinators is not known. Nectar, presumably present in only small amounts, and pollen are not readily accessible to insect visitors in the manner noted for bat-pollinated plants (Steiner, 1983). Phorids most likely forage opportunistically on a broad range of nutritive resources associated with the lowland tropical rain forest habitat. Some recent studies have shown, however, that relatively unspecialized dipteran pollinators can sustain high levels of fruit set in plant populations through their high numerical abundance, ability to thrive well under cool moist forest conditions, and relatively low energy demands (Mesler et al., 1980; Levesque and Burger, 1982). In the natural habitat of *Herrania,* phorids, rather than bees, would be the most effective pollinators due to their affinity for moist, shaded forest conditions, relatively low energy needs (relative to bees), and attraction to the aminoid scent of the flowers. Although bee pollination cannot be ruled out by this study, it seems that the elaborate pollination mechanism of *Herrania* is adapted principally to phorids as pollen vectors. Heavily-shaded forest understories are not conducive to bee pollination (e.g., Anderson and Beare, 1983). Yet some plant species have both "major" and "minor" pollinators (Lewis and Zenger, 1983) and the combined effects of both groups determine fruit set patterns. Phorids may be part of a primary group of insect pollinators associated with forests (Baumann, 1978). It is difficult, however, to conclude that the extant floral structure and physiology are adaptations to the extant pollinators, since other types of pollinators, no longer extant, might have been part of the original selection pressure underlying the coevolved association (Janzen, 1980).

In both *Theobroma* and *Herrania* the basic floral design is the same: the flower is hermaphroditic with a concave petal base and anthers alternating with stami-

nodes (see Cuatrecasas, 1964). Behaviorally, both the flowers of *T. cacao* and the *Herrania* species studied here follow similar diurnal cycles of anthesis and design of the floral reward system (e.g., Walker, 1959; Gorrez, 1962; Sampayan, 1966; Stejskal, 1969; Young et al., 1984). The inference in floral design for *T. cacao*, and presumably for other *Theobroma* species, has been selection away from selfing with stout staminodes preventing the transfer of pollen to the stigma and style of the same flower (see the review of Bystrak and Wirth, 1978). Extending such reasoning to *Herrania*, a closely allied genus, the possibility exists that most or all species are also self-incompatible. If this is the case, then the observed high abundance of fruit (relative to cacao) on species such as *H. purpurea* indicates that an apparently high abundance of phorids results in considerable transfer of pollen among different trees in the somewhat artificial setting typified by the "La Lola" garden. Experiments are underway to determine whether or not *H. purpurea* is self-incompatible, and to what degree are phorids capable of transferring pollen between trees at this locality. These studies will be conducted principally during the lengthy rainy season at "La Lola" since the dry season is a time of greatly reduced flowering in *Herrania* at this locality. The timing of flowering in tropical trees relative to prevailing rainfall patterns varies greatly in different climatic zones of Costa Rica (e.g., Opler et al., 1976), and the drier periods at "La Lola" appear to be more stressful to *Herrania* in terms of flowering.

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